

Comparative persistence of marine fish larvae from pelagic versus demersal eggs off southwestern Nova Scotia, Canada

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Abstract. Two groupings of larval fish were repeatedly identified by principal component analyses of larval densities from four broad-scale surveys during the spring and summer of 1985–1987 off southwestern Nova Scotia, Canada. Larvae originating from pelagic eggs (four species within Gadidae and Pleuronectidae) constituted one group, which were uniformly distributed over the sampling area with densities not correlated with bathymetry, although nearly all spawning occurs on the shallow western cap of Browns Bank, 100 km offshore. Larvae from demersal eggs (five species within Pholidae, Stichaeidae, Cottidae, Agonidae) constituted the second group, which dominated the shallow-water environments both inshore and on Browns Bank. Lower patchiness indices were evident amongst larvae from pelagic eggs in small and large sampling-gear collections (average 3.4 and 3.1, respectively) compared to fish hatching from demersal eggs (average 5.1 and 4.6). Fine-scale nearshore surveys over a 5 wk period in 1987 also showed that larvae of demersal eggs had a less variable distribution along an inshore-offshore transect. Larvae from demersal eggs appear spatially persistent through the release of well-developed larvae from non-drifting eggs. These conclusions are consistent with other studies over a range of spatial scales in temperate and tropical environments, demonstrating that single-species models of larval dispersal are inadequate to account for the distributional patterns of larval fish in general.

Introduction

A recent theoretical development to emerge in the population biology of marine fishes is the larval retention hypothesis (Iles and Sinclair 1982, Sinclair and Iles 1988). It maintains that fish larvae persist in geographically dis-

tinct areas through active vertical migration across a velocity shear. The theory was largely developed and supported from empirical observations of fall-spawned Atlantic herring larvae (*Clupea harengus*) in southwestern Nova Scotia. In this region, herring larvae appear to persist in the vicinity of the spawning area until the following spring, despite the dispersive effects of winter storms and strong tidal and residual currents (Sinclair and Iles 1985, Stephenson and Power 1988).

A generalised larval dispersal pattern based on herring is probably inappropriate. Herring larvae hatch from negatively buoyant, demersal (benthic) eggs that adhere to the substratum. Atlantic herring and other species with demersal eggs frequently spawn in nearshore waters (<30 km) where their larvae predominate (Chenoweth 1973, Richardson and Percy 1977, Able 1978, Minami and Tamaki 1980, Richardson et al. 1980). Consequently the eggs normally do not drift, and yolk-sac larvae are large (5 to 10 mm, especially in temperate species), with functional fins, eyes, and gut (Iwai 1980, Barlow 1981, Thresher 1984), all of which can have significant implications for their subsequent dispersal (Leis and Miller 1976, Leis 1982, Marliave 1986).

In contrast, many marine species have pelagic eggs that are released into the water column and are subject to passive dispersal by wind and tide-induced circulation. Pelagic eggs tend to be smaller than demersal eggs, or have shorter incubation times, and upon hatching release larvae that are often smaller (3 to 5 mm), with undeveloped fins and unpigmented eyes (Thresher 1984). These larvae may be subject to further passive dispersal before they become functionally competent. Many larvae from pelagic eggs in the tropics may also become morphologically distinctive, possessing spines and other pelagic characteristics that are lost upon settlement (Thresher 1984, Smith et al. 1987). Distributions of larvae from pelagic eggs are generally observed well offshore (>30 km), and have been described as a species guild on the Scotian Shelf (O'Boyle et al. 1984), as well as in the Sea of Japan (Minami and Tanaki 1980), off the northwest coast of Oregon (Richardson and Percy 1977), and in the

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tropical-reef environment (Leis and Miller 1976, Leis 1982, Smith et al. 1987).

Thus, general dispersal models for the early life stages of marine fish (e.g. Harden Jones 1968, Williams et al. 1984, Sinclair and Iles 1988) are often inadequate for other regions and species (O'Boyle et al. 1984, Cushing 1986, Kiørboe et al. 1988, Kingsford and Choat 1989, Suthers and Frank 1989, Taggart et al. 1989). Nearshore ichthyoplankton may be spatially persistent through the release of developed larvae from non-drifting eggs. In this study, we compare the horizontal distributions of larval fish hatching from pelagic and demersal eggs from four cruises during the spring and early summer of 1985–1987, in the shelf and nearshore waters of southwestern Nova Scotia. Our aims were to determine if larvae hatching from demersal eggs formed a distinctive ichthyoplankton community dominating the shallow-water environment. Larvae from pelagic eggs should comprise another community uniformly distributed over the survey area. We also wished to determine if larvae from demersal eggs exhibited a greater degree of geographic persistence near the spawning ground than larvae from pelagic eggs. The term "larval persistence" refers to the cohort, and not to the individual. Larvae from demersal eggs were predicted to exhibit higher degrees of aggregation, or patchiness (Lloyd 1967). We also compared the distributions of larvae from pelagic and demersal eggs in the nearshore environment of southwestern Nova Scotia which was sampled intensively during the spring of 1987.

Materials and methods

Study area and cruise dates

Four large-scale spring and early summer ichthyoplankton surveys were conducted in southwestern Nova Scotia from 1985 to 1987, which involved several cruises (Fig. 1, Table 1). The area is characterised by strong, tidal currents ($>90 \text{ cm s}^{-1}$), and a northerly residual flow ($5 \text{ to } 10 \text{ km d}^{-1}$, Smith 1989). Two sizes of sampling gear were used at each station. The small sampling gear used to collect fish larvae was either a mini-BIONESS (Bedford Institute of Oceanography net and environmental sensing system; 0.25 m^2 , $333 \mu\text{m}$ mesh) or a 0.5 m -diam ring net ($405 \mu\text{m}$ mesh). The size distributions of larval cod were compared between these two small sampling-gear types by Suthers and Frank (1989), and were found to be not significantly different. The mini-BIONESS sampled 5 to 7 depth intervals to a maximum of 55 m , which were combined as a weighted average at each station (total volume filtered at a towing speed of 1.5 m s^{-1} was about 1000 m^3). The 0.5 m -diam ring was towed obliquely from 20 m to the surface (volume filtered 300 m^3). The large sampling gear used to collect larger larvae was a Tucker trawl (effective opening 2.5 m^2 , $1600 \mu\text{m}$ mesh). The Tucker trawl was towed obliquely from 55 m to the surface (volume filtered was about 10000 m^3). Further details of sampling are given in Suthers and Frank (1989). The average larval density was calculated for replicated stations in three surveys (8 of 31 stations in Cruise 85-1; 15 of 55 stations in Cruises 86-1, 2; 9 of 54 stations in Cruise 86-3); stations in Cruise 87-2 were not replicated.

Nearshore sampling was conducted from 26 April until 2 June 1987, at seven stations 9 km apart along Latitude $43^\circ 45' \text{N}$, perpendicular to the coast (Cruise 87-1, Table 1). Only one gear type was used at each station, either a Tucker trawl or a 1.0 m -diam ring net ($1000 \mu\text{m}$ mesh). A Tucker trawl was used on 26–27 April, 3 May and 2 June. The 1.0 m ring net was used on the remaining seven

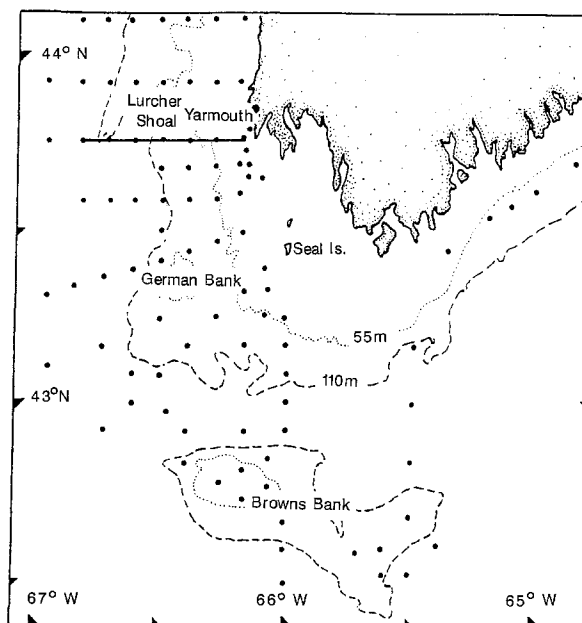


Fig. 1. Study area off southwestern Nova Scotia showing all stations (●) sampled on the four broad-scale surveys. Line connecting seven nearshore stations, 9 km apart, indicates transect sampled repeatedly on Cruise 87-1

Table 1. Cruise dates of four large-scale surveys in southwestern Nova Scotia, and nearshore survey sampling dates on Cruise 87-1 at stations spaced at 9 km along $43^\circ 45' \text{N}$. Bio: mini-BIONESS; 0.5 m : 0.5 m ring net; 1 m : 1 m diam ring net; Tt: Tucker trawl; N : no. of stations

Dates	Cruise	Gear	(N)
May 1985 survey 9–21 May	85-1	Bio, Tt	(30)
May 1986 survey 10–18 May	86-1	Bio, Tt	(35)
14–23 May	86-2	0.5 m , Tt	(20)
June 1986 survey 5–11 June	86-3	0.5 m , Tt	(54)
May 1987 survey 28 May–4 June	87-2	Bio, Tt	(54)
May 1987, nearshore survey 26–27 April	87-1	Tt	(8)
3 May		Tt	(7)
9 May		1 m	(7)
10 May		1 m	(5)
14 May		1 m	(7)
17 May		1 m	(7)
18 May		1 m	(7)
2 June	87-2	Tt	(7)

sampling dates (Fig. 1, Table 1). All sampling gear was towed at 1.5 m s^{-1} obliquely from 5 to 25 m , depending on water depth, filtering approx 10000 m^3 (Tucker trawl) and 2000 m^3 (1 m ring). All fish larvae were identified and their standard length was measured to the nearest 0.1 mm (up to 30 individuals per species per sample). In Cruise 86-3, only cod and haddock larvae were measured.

Analysis

We wished to determine if there were any repeatable, broad-scale patterns between the species collected on each cruise. The species \times station data matrix of larval densities was analysed by principal component analysis. For each cruise and gear type the first two, rotated (varimax) components indicated the relative species associations. Larval densities were transformed to natural logarithms, $\ln(x+1)$ to linearise the relationships. Component scores at each station were obtained by multiplying the standardised abundance data by the factor score coefficients. The spatial distribution of the component scores at each station was examined by Spearman rank correlation with bathymetry.

The large-scale distributions of each species within each cruise was evaluated using Lloyd's (1967) patchiness index derived from the mean (\bar{x}) and variance (s^2):

$$P = (\bar{x} + ((s^2/\bar{x}) - 1))/\bar{x}. \quad (1)$$

The index is similar to Morisita's index of dispersion; it is independent of the mean density, but strongly dependent on volume filtered and sample size (Elliot 1977). Therefore, the unit volumes used were the approximate volume sampled by each gear type. If the mean density for a given species was <1 (as the denominator in Eq. 1), the index was not evaluated. Spatial plots of the Tucker trawl samples (mostly pelagic juveniles) for each cruise were produced for the two most abundant species hatching from each egg type. The scale for the expanding symbols in the spatial plots was standardised at 50, 25, 10 and 5% of the maximum station abundance for each species. Contouring was not used due to the irregular boundary of the sampling grid. All analyses were performed using SYSTAT (Systat Incorporated, Version 4.0).

During spring 1987, nearshore larval distributions along the transect were compared by calculating the horizontal centre of mass of the station larval densities (nos. 1000 m^{-3}), as the weighted distance from shore (d_w) for each species on each sampling date;

$$d_w = \frac{\sum (\text{larval density} \times \text{distance})}{\sum \text{larval density}}. \quad (2)$$

The horizontal and temporal variability of this weighted distance (km) from shore, was determined from the weighted variance (s^2) for each species on each sampling date;

$$s^2 = \frac{\sum ((\text{distance} - d_w)^2 \times \text{larval density})}{\sum (\text{larval density})}. \quad (3)$$

Therefore, the greater the weighted variance, the greater the variability in the inshore-offshore distribution.

Larval density distributions along the transect over the 5 wk interval were contoured using the Kriging method (Clarke 1979), with contours for ichthyoplankton standardised at approximately 50, 25, 10, 5% and occasionally 2.5% of the maximum station abundance observed during the 5 wk period.

Results and discussion

Broad-scale ichthyoplankton community

Four larval species hatching from pelagic eggs occurred in the study area during each spring from 1985–1987: three gadids (Atlantic cod, *Gadus morhua*; haddock, *Melanogrammus aeglefinus*; and pollock, *Pollachius virens*) and one pleuronectid (American plaice, *Hippoglossoides platessoides*) (Table 2). Five species from demersal eggs were abundant (>1 per 1000 m^3): a pholid (rock gunnel, *Pholis gunnellus*), a stichaeid (radiated shanny, *Ulvaria subbifurcata*), two cottids (longhorn sculpin, *Myoxocephalus octodecemspinosus*, and grubby, *M. aeneus*), and one agonid (alligatorfish, *Aspidophoroides monoptyerygius*) (Table 2).

In all eight principal component analyses of the larval densities (4 surveys \times 2 gears), the first two components together accounted for 67 to 83% of the inter-station variance in larval density (Fig. 2). Plots of each species on the rotated components clearly separated species hatching from pelagic eggs and species hatching from demersal eggs (Fig. 2). One exception was in Cruise 87-2, BIONESS (Fig. 2 G), when rock gunnel were broadly distributed over the survey area. Thus, cod were intermediately located in this analysis.

The first two components could therefore be attributed to a pelagic egg component, or a demersal egg component (except in Fig. 2 G). The pelagic egg component-scores for each station were not significantly correlated with bathymetry (Fig. 3), while the demersal component-

Family and species	Spawning time and mode	
Gadidae	} pelagic spawning	
<i>Gadus morhua</i> (Atlantic cod)		Feb.–Apr.
<i>Melanogrammus aeglefinus</i> (haddock)		Apr.–May
<i>Pollachius virens</i> (pollock)	Nov.–Feb.	
Pleuronectidae	} pelagic spawning	
<i>Hippoglossoides platessoides</i> (American plaice)	Mar.–July	
Pholidae	} demersal spawning	
<i>Pholis gunnellus</i> (rock gunnel)	Jan.–Feb.	
Stichaeidae	} demersal spawning	
<i>Ulvaria subbifurcata</i> (radiated shanny)	May–June	
Cottidae	} demersal spawning	
<i>Myoxocephalus octodecemspinosus</i> (longhorn sculpin)		Dec.–Mar.
<i>M. aeneus</i> (grubby)		Dec.–Mar.
<i>M. scorpius</i> (shorthorn sculpin) ^a	Dec.–Mar.	
Agonidae	} demersal spawning	
<i>Aspidophoroides monoptyerygius</i> (alligatorfish)	Mar.–May?	
Clupeidae	} demersal spawning	
<i>Clupea harengus</i> (herring) ^a	Jul.–Aug.	

Table 2. Species collected during all surveys, their spawning mode and approximate spawning date in southwestern Nova Scotia. Spawning times are from Colton et al. (1979), and Scott and Scott (1988)

^a Collected during nearshore survey only

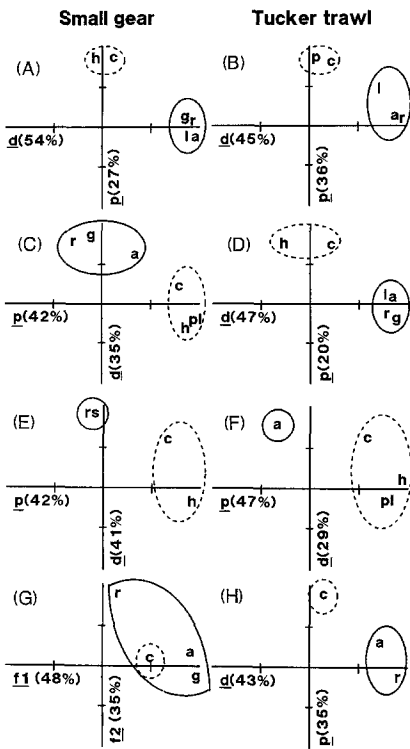


Fig. 2. Plots of eight principal-component analyses (4 surveys by 2 gears) for larval cod (c), haddock (h), pollock (p), American plaice (pl), rock gunnel (r), radiated shanny (rs), longhorn sculpin (l), grubby (g), alligatorfish (a) on first two rotated components, including percentages of the variance explained during Cruise 85-1 (A, B), Cruises 86-1, 2 (C, D), Cruise 86-3 (E, F) and Cruise 87-2 (G, H). Axes for each component are labelled pelagic (p), or demersal (d), based on magnitude of component loading (axes from -1 to $+1$); in (G) there was no clear distinction, so axes are labelled f_1 and f_2 . Species ringed with dashed lines have pelagic eggs, those ringed with continuous lines have demersal eggs. Full specific names in Table 2

scores and bathymetry were highly and negatively correlated. Larvae from demersal eggs therefore appear to form a distinctive ichthyoplankton community, dominating the shallow-water environment.

Large-scale distribution of larvae from pelagic eggs

Over 80% of the patchiness indices for larvae from pelagic eggs in both gear types were less than the overall mean value of 4.1 (Table 3). The average patchiness index from the small gear was $3.4 (\pm 1.3, 95\% \text{ confidence interval})$ and $3.1 (\pm 0.7)$ from the Tucker trawl. High patchiness in haddock larvae in the small gear during Cruise 86-1, 2 (Table 3, index = 6.5), was due to very high densities ($> 1 \text{ m}^{-3}$) in the gyre situated over the western cap of Browns Bank. An equally high patchiness index was not evident amongst haddock in the Tucker trawl at this time, suggesting that the high larval patchiness was short-lived (Table 3).

The actual spatial distributions of larvae from pelagic eggs in the Tucker trawl samples show that larvae generally occurred at all stations in the sampling area, and yet spawning by cod and haddock only occurs on Browns Bank at this time of year in southwest Nova Scotia (Hur-

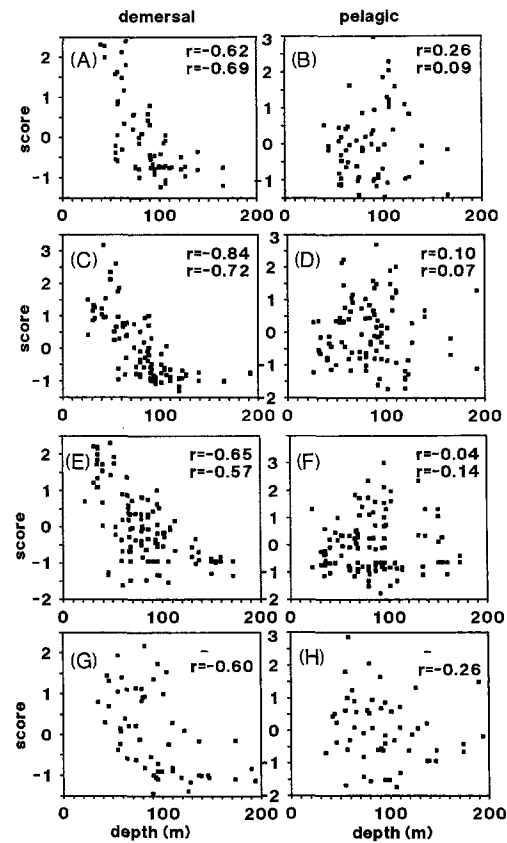


Fig. 3. Principal-component scores at each station for pelagic egg species (right column) and demersal egg species components (left column), plotted as a function of bathymetry for both gear types combined, on Cruise 85-1 (A, B), Cruises 86-1, 2 (C, D), Cruise 86-3 (E, F), and Cruise 87-2 (G, H). Spearman rank correlation coefficients between pelagic and demersal component scores and bathymetry are shown: upper coefficients = small gear, lower coefficients = Tucker trawl

ley and Campana 1989). Pollock and American plaice are also believed to spawn offshore during late winter-early spring (O'Boyle et al. 1984, Neilson et al. 1988). Larval cod were concentrated at the northernmost stations in 1985 (Fig. 4A), and in May 1987 occurred mainly on Browns Bank and the southwestern-most stations (see Fig. 7A). In May 1986, cod occurred both offshore on Browns Bank as well as inshore (Fig. 5A). Similarly, haddock larvae occurred on Browns Bank and at stations to the northwest in May 1986 (Fig. 5B) and in June 1986 (Fig. 6A). In June 1986, larval American plaice were broadly distributed throughout the sampling area (Fig. 6B). In summary, the spatial distribution plots, patchiness indices and the principal component analyses all indicate a broad and more uniform distribution of larvae hatching from pelagic eggs, despite the spawning area being only on Browns Bank.

Large-scale distribution of larvae from demersal eggs

In contrast to the larvae from pelagic eggs, $> 50\%$ of the patchiness indices derived for larvae from demersal eggs exceeded an overall mean value of 4.1 (compared to 19% of the pelagic egg indices, Table 3). The average patchi-

Table 3. Lloyd's (1967) patchiness indices (P), and mean density (dens.) collected by small gear (nos. 1000 m^{-3}) and Tucker trawl (nos. 10000 m^{-3}), for larvae from pelagic and demersal eggs off southwestern Nova Scotia. Mean P ($\pm 95\%$ confidence intervals) is average for each gear \times spawning-mode group. L: mean standard length (mm); -: insufficient or zero catch

Cruise and species	Small gear			Tucker trawl		
	P	dens.	L(mm)	P	dens.	L(mm)
Larvae from pelagic eggs						
Cruise 85-1						
cod	1.5	(2.1)	7.9	2.5	(6.6)	20.5
haddock	1.8	(1.9)	4.2	-	-	-
pollock	-	-	-	2.3	(1.8)	17.5
Cruises 86-1,2						
cod	2.7	(23.2)	7.7	2.8	(14.9)	17.0
haddock	6.5	(84.5)	5.9 ^a	3.2	(1.7)	10.6 ^a
plaice	3.8	(11.6)	7.4 ^a	-	(0.8)	-
Cruise 86-3						
cod	3.1	(1.2)	13.0	2.3	(5.4)	17.0
haddock	4.5	(2.8)	- ^b	2.6	(8.2)	10.2
plaice	-	-	-	3.3	(1.7)	-
Cruise 87-2						
cod	2.9	(1.0)	18.2	4.8	(12.7)	23.7
Mean P	3.4	(± 1.3)		3.1	(± 0.7)	
Larvae from demersal eggs						
Cruise 85-1						
rock gunnel	4.1	(5.5)	24.1	3.8	(3.8)	26.9
longhorn sculpin	3.2	(1.5)	10.5	2.9	(9.9)	12.5
grubby	9.6	(2.2)	6.4	-	-	-
alligatorfish	3.2	(1.6)	10.5	3.5	(3.3)	15.1
Cruise 86-1,2 ^a						
rock gunnel	8.8	(3.8)	28.6	3.8	(5.0)	30.3
longhorn sculpin	-	(0.8)	11.7	6.1	(7.2)	12.9
grubby	4.2	(5.0)	7.6	8.3	(5.4)	10.2
alligatorfish	5.0	(2.3)	15.8	5.5	(5.8)	18.0
Cruises 86-3						
alligatorfish	-	(0.4)	-	3.0	(2.3)	-
radiated shanny	4.8	(42.1)	-	-	-	-
Cruises 87-2						
rock gunnel	5.5	(1.7)	27.9	3.2	(2.5)	29.3
longhorn sculpin	-	-	-	6.9	(0.9)	16.2
grubby	4.2	(1.0)	6.6	-	(0.3)	-
alligatorfish	3.7	(2.6)	18.5	3.7	(7.4)	18.8
Mean P	5.1	(± 1.4)		4.6	(± 1.2)	

^a Lengths from Cruise 86-1 only

^b Not measured

ness index from the small gear was $5.1 (\pm 1.4, 95\%$ confidence interval) and $4.6 (\pm 1.2)$ from the Tucker trawl. Therefore, in general larvae hatching from demersal eggs have a more clumped distribution at the scale of 9 km between stations, than larvae from pelagic eggs.

The actual spatial distributions of larvae hatching from demersal eggs (Tucker trawl) show that, in contrast to larvae of pelagic eggs, they were distributed predominantly in shoal water on the western cap of Browns Bank, and inshore of the 110 m isobath, where spawning by these species is believed to occur (Scott and Scott 1988). In 1985 the distribution of rock gunnel and longhorn

sculpin occurred on the western cap of Browns Bank, and to the north between the 55 and 110 m isobath – although few stations were sampled beyond these depths (Fig. 4C, D). In May 1986 the majority of longhorn sculpin and grubbies occurred on the shallow western cap of Browns Bank, and along the 55 m isobath (Fig. 5C, D). Similarly, in June 1986 alligatorfish were abundant inshore of the 110 m isobath, with the highest densities at the <55 m isobath (Fig. 6C). In May 1987, while rock gunnel extended beyond the 110 m isobath, low densities were encountered at the offshore extremity (Fig. 7B). Alligatorfish during May 1987 were most abundant in shallow water; on the western cap of Browns Bank, and inshore of the 110 m isobath (Fig. 7C).

In summary, larvae hatching from demersal eggs exhibited a more clumped distribution near the shallow-water spawning areas, and were characterised by higher patchiness indices than larvae from pelagic eggs. The predominance of larvae from demersal eggs in the nearshore community observed in southwestern Nova Scotia, agrees with the spatial pattern observed in the northwest Atlantic (Chenoweth 1973, Able 1978) and northeast Pacific (Richardson and Percy 1977, Richardson et al. 1980).

Nearshore larval distribution, spring 1987

The most abundant nearshore species from pelagic eggs was cod. The temporal distribution of larval cod in spring 1987 (Fig. 8A) varied weekly along the transect, and on three occasions cod appeared to occur at the inshore and offshore ends of the transect. Pollock exhibited a similar distribution to cod when they occurred in early May (Fig. 8B). This varying horizontal and temporal distribution was quantified as the standard deviation of the weighted distance from shore for each sampling date, using for comparison an arbitrary value of ten. The standard deviation was nearly always >10 for the two species with pelagic eggs (Fig. 9A, B).

In contrast, the distribution of larval Atlantic herring and rock gunnel (from demersal eggs) was highly aggregated at the most inshore station in late April and early May (Fig. 8C, D). Larvae of the two sculpin species (Fig. 8E, F) were distributed in a discrete band between 10 and 30 km offshore, with a tendency to occur in deeper water by late May. Sea raven, *Hemitripterus americanus*, exhibited a similar distribution pattern to the other sculpins (Suthers unpublished data). The more discrete and temporally stable distributions along the transect of herring, rock gunnel and two sculpins, compared to cod and pollock, was indicated by their smaller standard deviations about the weighted distance from shore (Fig. 9).

Possible mechanisms for regulating larval distribution

Larvae from demersal eggs may persist off southwestern Nova Scotia through vertical migration across the vertical velocity shear that occurs close to the substrate (Lough and Trites 1989). Efficient swimming behaviour is

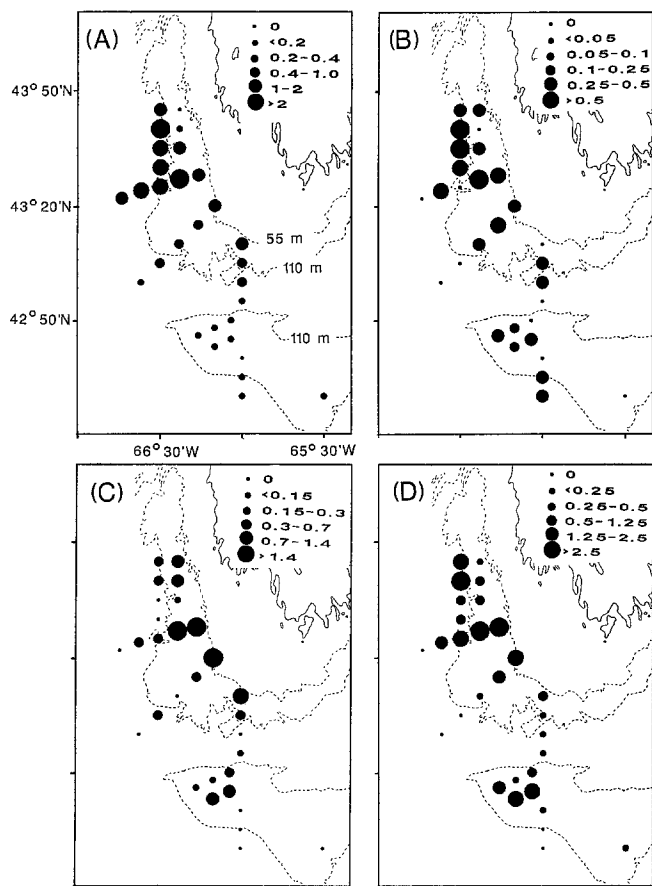


Fig. 4. Distributions (nos. 1000 m^{-3}) of larval Atlantic cod (A), pollock (B), rock gunnel (C), and longhorn sculpin (D) determined with Tucker trawl during Cruise 85-1

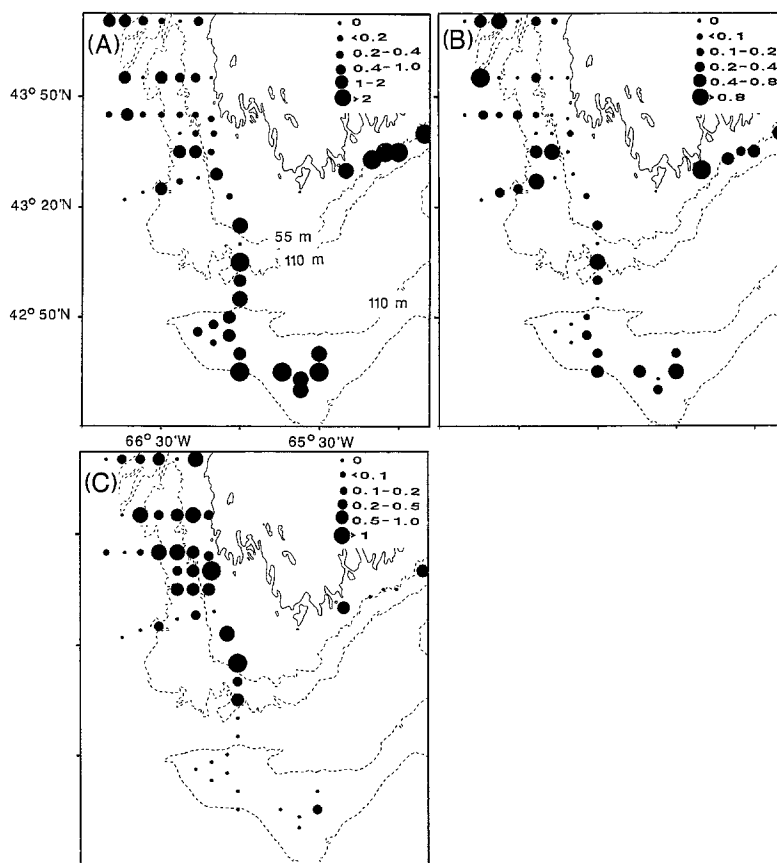


Fig. 6. Distributions (nos. 1000 m^{-3}) of larval haddock (A), American plaice (B), and alligatorfish (C) determined with Tucker trawl during Cruise 86-3

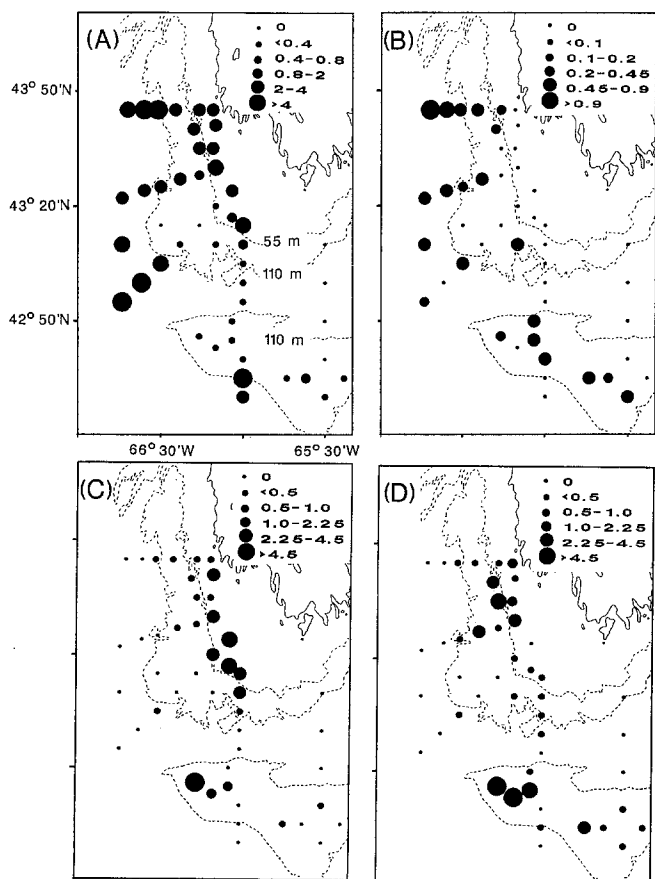


Fig. 5. Distributions (nos. 1000 m^{-3}) of larval Atlantic cod (A), haddock (B), grubby (C), and longhorn sculpin (D) determined with Tucker trawl during Cruises 86-1,2

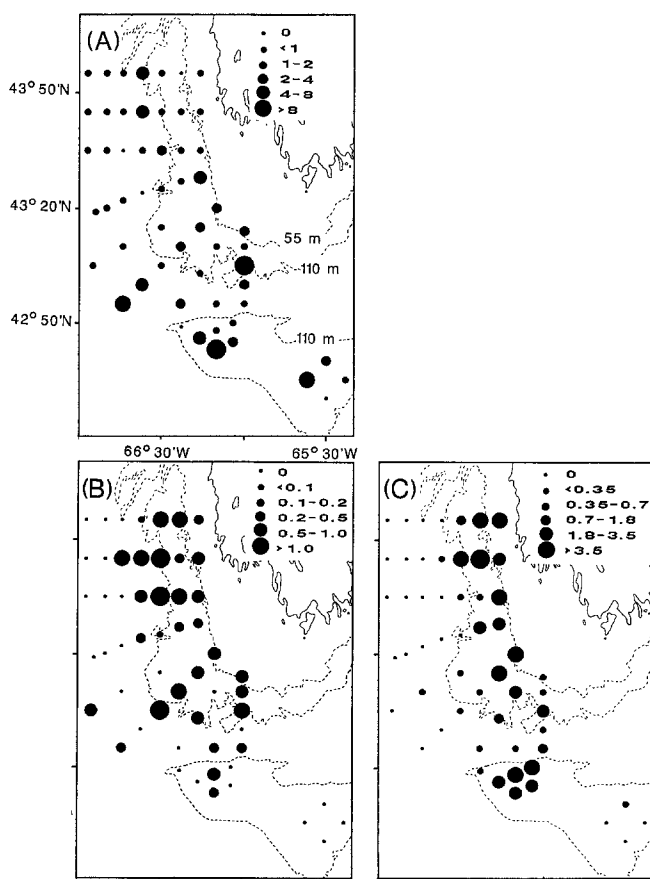


Fig. 7. Distributions (nos. 1000 m^{-3}) of larval Atlantic cod (A), rock gunnel (B), and alligatorfish (C) determined with Tucker trawl during Cruise 87-2

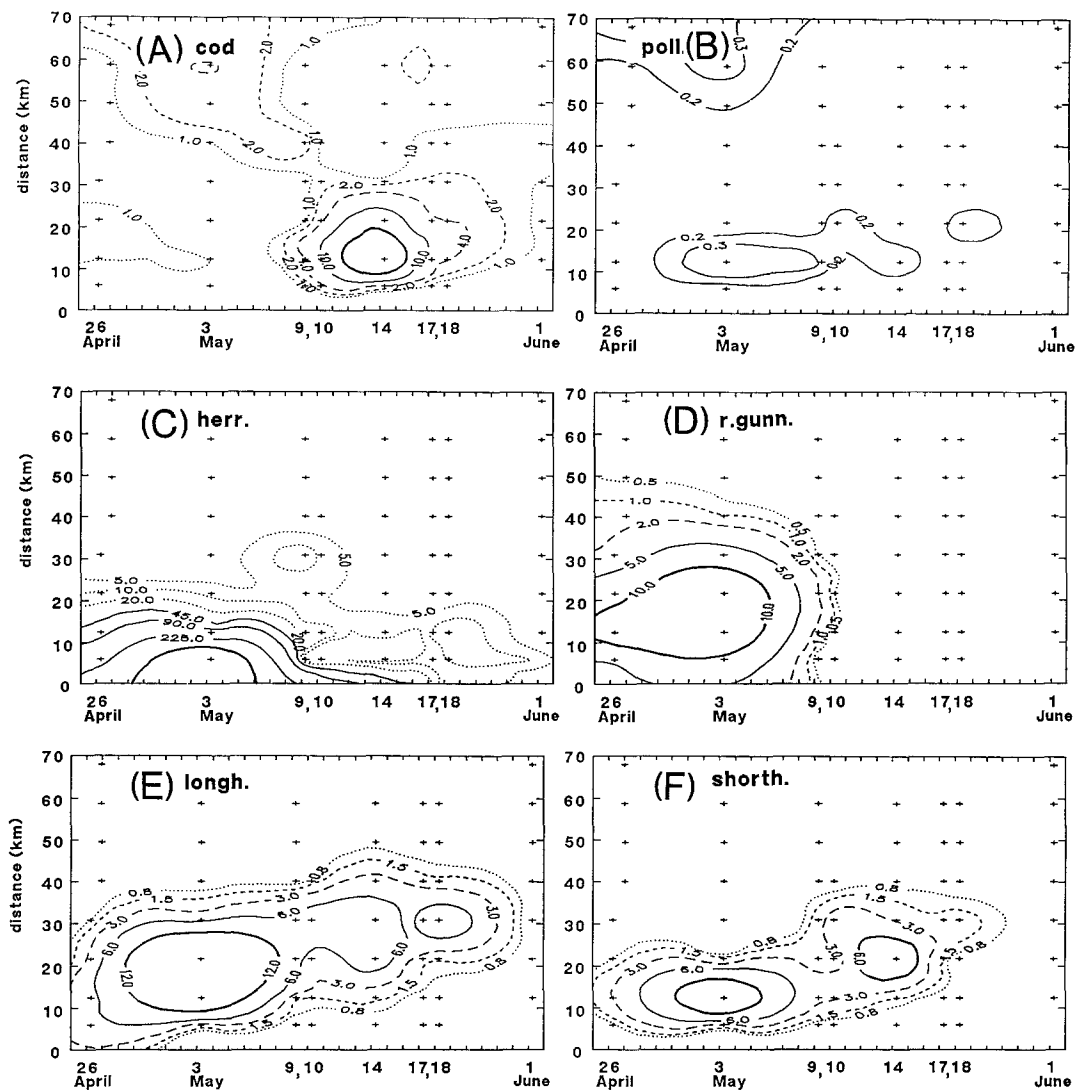


Fig. 8. Horizontal distributions (nos. 1000 m^{-3}) of larval Atlantic cod (A), pollock (B), Atlantic herring (C), rock gunnel (D), longhorn sculpin (E), and shorthorn sculpin (F) along nearshore

transect of Cruise 87-1. Contours set at approx 50, 25, 10, 5, and 2.5% of maximum station abundance. (C) includes 1 and 0.5% of maximum station abundance

possible for larger larvae. For larvae $< 5\text{ mm}$ in length, Weigh (1980, after Blake 1983) showed that low Reynolds numbers predominate, and continuous swimming is the most efficient form of locomotion. Larvae $> 5\text{ mm}$ experience mainly inertial effects and burst-and-glide swimming becomes more efficient, such that by 15 mm the energy gain by this mode is of the same order as that predicted for adult fish (Blake 1983). Cod and pollock (pelagic eggs) hatch between 3 and 6 mm total length (Fahay 1983), while larvae from demersal eggs hatch at a larger size: rock gunnel 9 to 10 mm, herring 6 to 10 mm, sculpins 6.3 to 14 mm total length (Fahay 1983, Townsend 1983). Therefore, large size at hatching, and the more advanced stage of development of larvae from demersal eggs may account for their tendency to remain within a given area by superior swimming and sensory abilities. Size of fish larvae has been shown to be positively related to survival potential, sensory capabilities and, in particular, to burst and average swimming speed (Miller et al. 1988).

In southwestern Nova Scotia, herring larvae exhibit diel or semi-diel (tidal) vertical migration (Stephenson and Power 1988), with densities in benthic sled tows as high as those in oblique tows (Stephenson and Power 1989). Sculpin larvae in the coastal waters of the north-east Pacific also exhibited diel vertical migration (Marliave 1981) and, as in herring larvae (Stephenson and Power 1988), this was considered to both regulate planktonic drift and maximise feeding opportunities.

On the other hand, gadid larvae exhibit little or no diel vertical migratory behaviour (Tilseth and Ellertsen 1984, Kendall et al. 1987, Frank et al. 1989), or the vertical migration observed is of unknown significance in influencing transport (Boehlert et al. 1985, Koeller et al. 1986, Perry and Neilson 1988). The variable horizontal distributions of larval ($< 10\text{ mm}$ standard length) and post-larval cod in this study support a similar conclusion for individual cod based on their age-structure and growth history determined from otoliths (Suthers et al. 1989). The hatch-date distributions of cod at nearshore

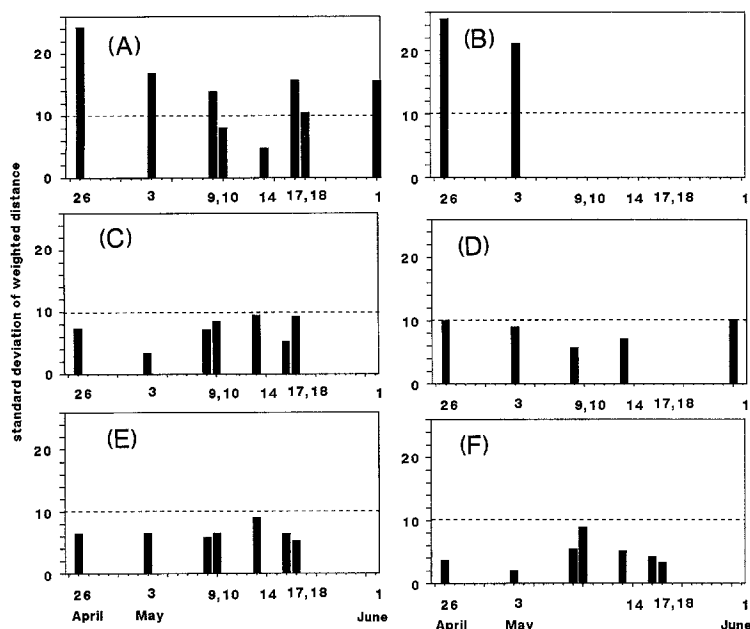


Fig. 9. Frequency histogram of standard deviation (s) of weighted distance from shore (km) on each sampling date during Cruise 87-1 for Atlantic cod (A), pollock (B), Atlantic herring (C), rock gunnel (D), longhorn sculpin (E), and shorthorn sculpin (F). Dashed horizontal lines indicate arbitrary standard deviation of 10 for comparison

stations were significantly different between cruises in May and June 1986, suggesting advection, differential mortality, or both. However, the hatch-date distributions were not significantly different between May and June 1986 for cod sampled on Browns Bank, which were retained within the gyre. Furthermore, the growth histories of nearshore cod (determined from the outer increments of otoliths) converged with that of Browns Bank cod at 3 and 4 wk pre-capture, indicating advection from a common origin (Suthers et al. 1989).

Larvae hatching from demersal eggs in other environments

Persistent distributions of larvae from demersal eggs have been documented over a range of spatial scales (m to km) in other temperate and tropical environments. Larvae from demersal eggs predominate in shallow coastal and estuarine environments on both the east and west coasts of North America (Chenoweth 1973, Richardson and Percy 1977, Able 1978). The prevalence of demersal spawning fish on the west coast in comparison to pelagic spawning congeners on the east coast, appears to be associated with vigorous upwelling and offshore Ekman transport that occurs on the west coast (Norcross and Shaw 1984).

At a finer spatial scale on the Canadian west coast, the concentration of cottid, stichaeid, and gobiesocid larvae from demersal eggs was two orders of magnitude greater within 1–2 m from shore, compared to 10–100 m offshore (Marliave 1986). These larvae also had a restricted longshore distribution, favouring a boulder shoreline over sand. In contrast, larvae derived from pelagic eggs (mostly gadids and pleuronectids) were more uniformly distributed both long-shore and cross-shore (Marliave 1986).

At a similar fine scale in New Zealand, Kingsford and Choat (1989) also observed that larvae from demersal

eggs were abundant near reef habitats of the adults, which was not observed for larvae from pelagic eggs. Moreover, patches of larval sparids (from pelagic eggs) appeared comparatively variable over a 3 d period, similar to observations for post-larval cod in southwestern Nova Scotia. However, Kingsford and Choat noted that the pelagic-demersal distinction was not consistent, as the distribution of larval blenniids and monocanthids (demersal spawning) was not influenced by the proximity of reefs.

In tropical regions, larvae from demersal eggs are also found closer inshore than larvae from pelagic eggs (Leis and Miller 1976, Leis 1982). The latter group in particular often possess morphological features that disappear upon settlement, such as elongate fin spines, cranial bone development, eye-shape, trailing hindgut and pigmentation (Smith et al. 1987). Examples include the leptocephalus of eels, the acronus larvae of acanthuroids and the tichlichthys larvae of the chaetodontids. Leis (1982, p. 89) concluded “that the most offshore pattern” [predominantly larvae from pelagic eggs] “was due to passive drift, while the inshore patterns” [predominantly larvae from demersal eggs] “were maintained by active swimming in conjunction with favourable currents”. Leis presented evidence of a tidal eddy and nearshore upwelling off the island of Ohau, Hawaii, as the putative mechanisms for inshore persistence of larvae derived from demersal eggs.

Consequences of persistent distributions

Recruitment variation of species with demersal eggs may be less than that of species with pelagic eggs, if larvae from demersal eggs are not as susceptible to unfavourable advection. In a review of recruitment variation in 30 marine fish stocks (Rothschild and DiNardo 1987), few stocks with demersal eggs were included, but the hypothesis of consistent recruitment is not well

supported. Other factors, such as age-structure, longevity, spawning duration and larval duration could be expected to influence recruitment variation as well. Lambert and Ware (1984) suggested that herring and capelin, with the "bet-hedging" reproductive strategy of protracted (demersal) spawning could produce stability in population size, compared to the "all at once" (pelagic) egg release by mackerel and hake. Obviously many factors influence recruitment, but the relative geographic persistence of larvae from demersal eggs may be an important component.

Persistent distributions of larvae from demersal eggs implies that migration of individuals and gene flow may be restricted between populations. It is noteworthy that the majority of "stock-rich species" identified by Sinclair and Iles (1988), including herring, capelin, smelt, Atlantic salmon, all produce demersal eggs. Higher levels of heterozygosity are found in a few demersal spawning species, particularly in species where larvae are also demersal (Bell et al. 1982, Thresher 1984, Waples 1987). Other electrophoretic studies of demersal spawning species concluded from the low levels of heterozygosity that there was little evidence of local endemism (e.g. Smith and Fujio 1982, Shacklee 1984), which indicates either recent geographic separation, or larval mixing by even just a few individuals.

Conclusions

Alternative physical mechanisms that account for the persistence of either larval group include the re-suspension of particles during the flood tide within estuaries (De Wolf 1973) or passive retention within gyres and eddies (e.g. Lobel and Robinson 1988). However, the occurrence of relatively stable distributions of ichthyoplankton off the southwestern coast of Nova Scotia which were consistent over four surveys is remarkable, considering its turbulent and dynamic nature. In contrast, the distributions of gadid and pleuronectid larvae from pelagic eggs appear more variable and more uniformly distributed. The cod were apparently advected from the natal Browns Bank gyre (Suthers and Frank 1989), and thus may be outside their environmental range (i.e., "vagrants" *sensu* Sinclair and Iles 1988). Alternatively, these results suggest a simple dichotomy in the behaviour and dispersal of marine fish larvae at the primary level of spawning mode. It is evident that general models of larval dispersal (Harden Jones 1968, Williams et al. 1984, Sinclair and Iles 1988) do not account for specific early life histories of all fish. The distinction in distribution pattern between larvae hatching from pelagic and demersal eggs is evident in many temperate and tropical studies. Perhaps the greater ability of larvae from demersal eggs to persist in local, coastal environments may contribute to their richer stock structure (Sinclair and Iles 1988) in comparison with larvae of pelagic egg origin.

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Literature cited

- Able, K. W. (1978). Ichthyoplankton of the St. Lawrence estuary: composition, distribution and abundance. *J. Fish. Res. Bd Can.* 35: 1518–1531
- Barlow, G. W. (1981). Patterns of parental investment, dispersal and size among coral-reef fishes. *Envir. Biol. Fish.* 6: 65–85
- Bell, L. J., Moyer, J. T., Numachi, K. (1982). Morphological and genetic variation in Japanese populations of the anemonefish *Amphiprion clarkii*. *Mar. Biol.* 72: 99–108
- Blake, R. W. (1983). *Fish locomotion*. Cambridge University Press, Cambridge
- Boehlert, G. W., Gadomski, D. M., Mundy, B. C. (1985). Vertical distribution of ichthyoplankton off the Oregon USA coast in the spring and summer. *Fish. Bull. U.S.* 83: 611–622
- Chenoweth, S. B. (1973). Fish larvae of the estuaries and coast of central Maine. *Fish. Bull. U.S.* 71: 105–113
- Clarke, I. (1979). *Practical geostatistics*. Elsevier Applied Science, London and New York
- Colton, J. B., Smith, W. G., Kendall, A. W., Berrien, P. L., Foy, M. P. (1979). Principle spawning areas and times of marine fishes, Cape Sable to Cape Hatteras. *Fish. Bull. U.S.* 76: 911–915
- Cushing, D. H. (1986). The migration of larval and juvenile fish from spawning ground to nursery ground. *J. Cons. int. Explor. Mer* 43: 43–49
- De Wolf, P. (1973). Ecological observations on the mechanisms of dispersal of barnacle larvae during planktonic life and settling. *Neth. J. Sea Res.* 6: 1–129
- Elliot, J. M. (1977). Some methods for the statistical analysis of samples of benthic invertebrates. 2nd ed. *Scient. Publ. Freshwat. biol. Ass.* 25: 1–160
- Fahay, M. P. (1983). Guide to the early stages of marine fishes occurring in the western North Atlantic Ocean, Cape Hatteras to the Southern Scotian Shelf. *J. NW. Atlant. Fish. Sci.* 4: 1–423
- Frank, K. T., Page, F. H., McRuer, J. R. (1989). Hydrographic effects on the vertical distribution of haddock (*Melanogrammus aeglefinus*) eggs and larvae on the southwestern Scotian Shelf. *Can. J. Fish. aquat. Sciences* 46(Suppl. 1): 82–92
- Harden Jones, J. R. (1968). *Fish migration*. Arnold, London
- Hurley, P. C. F., Campana, S. E. (1989). The distribution and abundance of haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhua*) eggs and larvae in waters off southwest Nova Scotia. *Can. J. Fish. aquat. Sciences* 46(Suppl. 1): 103–112
- Iles, T. D., Sinclair, M. (1982). Atlantic herring: stock discreteness and abundance. *Science, Wash., DC* 215: 627–633
- Iwai, T. (1980). Sensory anatomy and feeding of fish larvae. *Proc. 5th int. Center living aquat. Resour. Mgmt (ICLARM) Conf.* 5: 124–145. [Bardach, J. E., Magnuson, J. J., May, R. C., Reinhart, J. M. (eds.) ICLARM, Manila]
- Kendall, A. W., Clarke, M. E., Yoklavich, M. M., Boehlert, G. W. (1987). Distribution, feeding, and growth of larval walleye pollock, *Theragra chalcogramma*, from Shelikof Strait, Gulf of Alaska. *Fish. Bull. U.S.* 85: 499–521
- Kingsford, M. J., Choat, J. H. (1989). Horizontal distribution patterns of presettlement reef fish: are they influenced by the proximity of reefs. *Mar. Biol.* 101: 285–297
- Kjørboe, T., Munk, P., Richardson, K., Christiansen, V., Paulsen, H. (1988). Plankton dynamics and larval herring growth, drift and survival in a frontal area. *Mar. Ecol. Prog. Ser.* 44: 205–219
- Koeller, P. A., Hurley, P. C. F., Perley, P., Neilson, J. D. (1986). Juvenile fish surveys on the Scotian Shelf: implications for year-class size estimates. *J. Cons. int. Explor. Mer* 43: 59–76
- Lambert, T. C., Ware, D. M. (1984). Reproductive strategies of demersal and pelagic spawning fish. *Can. J. Fish. aquat. Sciences* 41: 1565–1569

- Leis, J. M. (1982). Nearshore distributional gradients of larval fish (15 taxa) and planktonic crustaceans (6 taxa) in Hawaii. *Mar. Biol.* 72: 89–97
- Leis, J. M., Miller, J. M. (1976). Offshore distributional patterns of Hawaiian fish larvae. *Mar. Biol.* 36: 359–367
- Lloyd, M. (1967). Mean crowding. *J. Anim. Ecol.* 36: 1–30
- Lobel, P. S., Robinson, A. R. (1988). Larval fishes and zooplankton in a cyclonic eddy in Hawaiian waters. *J. Plankton Res.* 10: 1209–1223
- Lough, R. G., Trites, R. W. (1989). Chaetognaths and oceanography on Georges Bank. *J. mar. Res.* 47: 343–369
- Marliave, J. B. (1981). Vertical migrations and larval settlement in *Gilbertidia sigalutes*, F. Cottidae. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer* 178: 349–351
- Marliave, J. B. (1986). Lack of planktonic dispersal of rocky intertidal fish larvae. *Trans. Am. Fish. Soc.* 115: 149–154
- Miller, T. J., Crowder, L. B., Rice, J. A., Marschall, E. A. (1988). Larval size and recruitment mechanisms in fishes: toward a conceptual framework. *Can. J. Fish. aquat. Sciences* 45: 1657–1670
- Minami, T., Tamaki, T. (1980). Offshore and nearshore distributional patterns of fish larvae along the San-in coast, the Sea of Japan. *Jap. J. Ichthyol.* 27: 156–164
- Neilson, J. D., DeBlois, E., Hurley, P. C. F. (1988). Stock structure of Scotian Shelf flatfish as inferred from ichthyoplankton survey data and the geographic distribution of mature females. *Can. J. Fish. aquat. Sciences* 45: 1674–1685
- Norcross, B. L., Shaw, R. F. (1984). Oceanic, coastal and estuarine transport of pelagic eggs and larvae with emphasis on fish: a review. *Trans. Am. Fish. Soc.* 113: 153–165
- O'Boyle, R. M., Sinclair, M., Conover, R. J., Mann, K. H., Kohler, A. C. (1984). Temporal and spatial distribution of ichthyoplankton communities of the Scotian Shelf in relation to biological, hydrological, and physiographic features. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer* 183: 27–40
- Perry, R. I., Neilson, J. D. (1988). Vertical distributions and trophic interactions of age-0 Atlantic cod and haddock in mixed and stratified waters of Georges Bank. *Mar. Ecol. Prog. Ser.* 49: 199–214
- Richardson, S. L., Laroche, J. L., Richardson, M. D. (1980). Larval fish assemblages and associations in the north-east Pacific Ocean along the Oregon coast, winter-spring 1972–1975. *Estuar. cstl mar. Sci.* 11: 671–699
- Richardson, S. L., Pearcy, W. A. (1977). Coastal and oceanic fish larvae in an area of upwelling off Yaquina Bay, Oregon. *Fish. Bull. U.S.* 75: 125–145
- Rothschild, B. J., DiNardo, G. T. (1987). Comparison of recruitment variability and life history data among marine and anadromous fishes. *Am. Fish. Soc. Symp.* 1: 531–546
- Scott, W. B., Scott, M. G. (1988). Atlantic fishes of Canada. *Can. Bull. Fish. aquat. Sciences* 219: 1–731
- Shacklee, J. B. (1984). Genetic variation and population structure in the damselfish, *Stegastes fasciolatus*, throughout the Hawaiian Archipelago. *Copeia* 1984: 629–642
- Sinclair, M., Iles, T. D. (1985). Atlantic herring (*Clupea harengus*) distributions in the Gulf of Maine-Scotian Shelf area in relation to oceanographic features. *Can. J. Fish. aquat. Sciences* 42: 880–887
- Sinclair, M., Iles, T. D. (1988). Population richness of marine fish species. *Aquat. living Resour. (Nantes)* 1: 71–83
- Smith, C. L., Tyler, J. C., Stillman, L. (1987). Inshore ichthyoplankton: a distinctive assemblage? *Bull. mar. Sci.* 41: 432–440
- Smith, P. C. (1989). Circulation and dispersion on Browns Bank. *Can. J. Fish. aquat. Sciences* 46: 539–559
- Smith, P. J., Fujio, Y. (1982). Genetic variability in marine teleosts: high variability in habitat specialists and low variability in habitat generalists. *Mar. Biol.* 69: 7–20
- Stephenson, R. L., Power, M. J. (1988). Semidiel vertical movements in Atlantic herring *Clupea harengus* larvae: a mechanism for larval retention? *Mar. Ecol. Prog. Ser.* 50: 3–11
- Stephenson, R. L., Power, M. J. (1989). Observations on herring larvae retained in the Bay of Fundy: variability in vertical movements and position of the patch edge. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer* 191: 177–183
- Suthers, I. M., Frank, K. T. (1989). Inter-annual distributions of larval and pelagic juvenile cod (*Gadus morhua*) in southwestern Nova Scotia determined with two different gear types. *Can. J. Fish. aquat. Sciences* 46: 591–602
- Suthers, I. M., Frank, K. T., Campana, S. C. (1989). Spatial comparison of recent growth in post-larval cod (*Gadus morhua*) off southwestern Nova Scotia: inferior growth in a presumed nursery area. *Can. J. Fish. aquat. Sciences* 46 (Suppl. 1): 113–124
- Taggart, C. T., Drinkwater, K. F., Frank, K. T., McRuer, J., Larouche, P. (1989). Larval fish, zooplankton community structure, and physical dynamics at a tidal front. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer* 191: 184–194
- Thresher, R. E. (1984). Reproduction in reef fishes. *Tropical Fish Hobbyist Publications Inc., Neptune City, New Jersey*
- Tilseth, S., Ellertsen, B. (1984). The detection and distribution of larval Arcto-Norwegian cod, *Gadus morhua*, food organisms by an in situ particle counter. *Fish. Bull. U.S.* 82: 141–156
- Townsend, D. W. (1983). The relations between larval fishes and zooplankton in two inshore areas of the Gulf of Maine. *J. Plankton Res.* 5: 145–173
- Waples, R. S. (1987). A multispecies approach to the analysis of gene flow in marine shore fishes. *Evolution* 41: 385–400
- Williams, D. McB., Wolanski, E., Andrews, J. C. (1984). Transport mechanism and the potential movement of planktonic larvae in the central region of the Great Barrier Reef. *Coral Reefs* 3: 229–236